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THE EFFECT OF SOME PUGET SOUND BOG WATERS ON THE ROOT HAIRS OF TRADESCANTIA

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The theory advanced in this paper is that plants other than bog xerophytes are excluded from peat bogs because of their inability to produce normal root hairs in the toxic habitat of bogs, their absorptive surface being thus so decreased that they cannot get water enough to enable them to live. The writer has also confirmed with Puget Sound bog waters certain results obtained by other workers with bog waters from the Middle West and extreme East.

Description of bogs

The xerophilous character of the flora of peat bogs is well known. In the Puget Sound region the plants most characteristic of undrained bogs are *Ledum groenlandicum*, *Kalmia glauca*, *Oxycoccus oxycoccus intermedius*, *Sphagnum*, and *Drosera rotundifolia*. The first four plants named are found in every undrained bog that the author has visited in the region, while the last one has been found absent from a few. Other plants sometimes found in bogs of the region are *Pinus monticola*, *Betula glandulosa*, *Salix myrtilloides*, *Myrica Gale*, *Eriophorum russeolum*, and *Juncus oregana*. *Tsuga heterophylla* and *Pinus contorta* are found on the drier hummocks in bogs (8), *Ledum columbianum* and *Myrica californica* are reported to be found in the beach bogs along the Pacific Ocean instead of *L. groenlandicum* and *M. Gale* (8).

Peat bogs are common in the Puget Sound region. The studies reported in this paper are based on six bogs. One of these is situated within the city of Seattle at the corner of E. 55th St. and 6th Ave. N.E. During the last two years the forest surrounding this bog has been cleared away and the streets along its edges have been filled with dirt from the neighboring hills. It has not been drained however and its flora is still just as typical as it was before the surrounding forest was removed, except that *Drosera*
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rotundifolia has disappeared, which was fairly common in this bog in 1908. It is a small bog, about 100 by 200 m. in extent. For convenience it will be referred to as the Seattle bog.

The largest bog studied is situated about 1760 m. east of Henry Station on the Seattle-Everett interurban railway. The undrained portion of this bog is perhaps 16 hectares in area, and its flora is typical, including *Drosera*. In addition to the usual bog plants, *Pinus monticola* is common, and *Trientalis arctica* is found along the border. The natural contour of the region is such that there is some drainage from the northern end of this bog into a small creek, and that portion of it lacks *Drosera* and *Pinus* and has *Lysichiton kamschatcense*. This bog will be referred to as the Henry bog.

The bog situated about 5280 m. southeast of Fauntleroy Park in Seattle is a little smaller than the Henry bog. Its area is estimated at about 10 hectares. *Drosera* is abundant in it, and *Trientalis arctica* is common along its margin. This bog will be designated as the Fauntleroy bog.

The bog situated at Echo Lake station on the Seattle-Everett interurban railway is slightly smaller even than the Seattle bog. It is on the margin of Echo Lake and its edge forms the bank of the lake for a short distance. The bog flora is typical right up to the open water of the lake; *Drosera* is abundant, and *Comarum palustre* is found on the border of the lake immediately adjacent to the bog. This bog will be called the Echo Lake bog. It is about 8800 m. distant from the Henry bog.

The bog that will be referred to as the Green Lake bog is situated just north of the city limits of Seattle. It is a little over 1760 m. north of Green Lake, which is entirely within the city limits. There is now remaining only about 0.4 hectare of this bog; formerly it was about 12 hectares in extent, but nearly all of it has been stripped of its original vegetation and drained. A good deal of it has been divided into small garden tracts and some of these are now under cultivation. The uncleared portion is drained by roadside ditches on two sides; water flows freely from the bog into one of these ditches during the rainy season and there is considerable seepage into the other one. This bog still has the typical bog

plants of the region, including *Drosera*. In addition to these, however, it contains the following plants not usually found in bogs: *Pseudotsuga taxifolia*, *Picea sitchensis*, *Thuja plicata*, *Tsuga heterophylla*, *Alnus oregona*, *Comarum palustre*, *Lysichiton kamtschaticense*, a *Carex*, and a small orchid. It will be noted that some of them (e.g., *Lysichiton kamtschaticense*) are found on the borders of other bogs, and that one of them (*Tsuga heterophylla*) is found on the dry hummocks in other bogs. Apparently the partial drainage here has allowed the entrance of plants not found in typical bogs, but has not driven out the typical bog plants.

The last of the six bogs is situated on Mount Constitution at an elevation of about 666 m.; the mountain itself attains a height of 880 m. It is situated on Orcas Island, one of the San Juan group, which lies between the strait of Juan de Fuca and the strait of Georgia. Several peat bogs situated on this mountain have been drained and thus converted into meadows, which have been used for both hay and pasturage. Drainage and clearing seem to have completely destroyed the bog flora and substituted a flora not at all characteristic of peat bogs.

The bog water for use in the experiments has been obtained in all cases as follows. Care was first taken to select a spot that was centrally located in the bog and had a typical bog flora. The mass of vegetation and fibrous peat was cut away with a strong knife from an area about one foot square. Then the soft peat was scooped out below this until a cavity was formed that would soon fill with water. The water was dipped up in a wide-mouth glass bottle and poured into glass containers. The depth to which this had to be scooped out varies with the season; in winter about 35 cm. sufficed in most of the bogs; in late summer it was necessary to dig 90 cm. In the case of the water obtained from the Henry bog on October 10, 1911, it was found that it would not accumulate in half an hour by digging even 90 cm. deep, and a glass jar was filled with very wet peat and the water was squeezed through cheesecloth in the laboratory.

The tap water used was that supplied to the laboratories from a wooden supply tank on the University campus. It is pumped into this tank from Lake Washington.

The expression "normal root hairs" used in this paper with reference to *Tradescantia* (the species common in greenhouses, and known as wandering Jew) means such root hairs as grow on the roots of cuttings in tap water. These hairs cover the entire surface of the root even when it reaches a length of 70 mm. or more. They are almost uniformly distributed, 4 mm. or more in length, mostly straight, and appear to the naked eye like somewhat silky fibers. Over 200 specimens of this plant grown in tap water have been examined and there has been found practically no variation from this description.

Investigation

In October 1909 experiments were begun on the germination of wheat, corn, beans, and peas in moist peat and between sheets of moistened blotting paper. It was found that these seeds germinated just as readily when the moisture was furnished by bog water as when it was furnished by tap water.

In the fall of 1910 *Ledum groenlandicum* and *Kalmia glauca* were propagated by cuttings in both bog water and tap water in the laboratory. Young roots from both of these species from both kinds of water were examined and found to be entirely devoid of root hairs. Some of the roots examined were produced on old roots formed before the plants were removed from the bog and some were produced on stems.

TRANSEAU (10) found root hairs absent in *Oxycoccus macrocarpus*. He also found that the roots of *Larix laricina* were "composed of mycorrhiza," and that their cortical tissues were early destroyed by a fungus. When he grew these plants in a well-aerated culture solution "normal roots with root hairs were produced."

COVILLE (1) found *Vaccinium corymbosum* to be devoid of root hairs. He found also that the walls of the epidermal cells of the roots were 1.3–2.5 μ thick, this being four to six times as thick as the walls of epidermal cells of wheat roots. He computes that a given section of wheat root presents about ten times as much absorptive surface as a section of blueberry (*Vaccinium corymbosum*) root of the same area.

In the fall of 1909 and again in 1910-1911 experiments were conducted on the effect of bog water on the production of root hairs on cuttings of *Tradescantia*. The experiments reported in the following table were carried out in 1910-1911 in 150 cc. glass bottles with extra wide mouths.

TABLE I
THE PRODUCTION OF ROOT HAIRS ON TRADESCANTIA IN BOG WATER

	NO. OF PLANTS USED	ROOT HAIRS			
		Normal	Slightly stunted	Much stunted	None
Seattle bog.....	16	..	3	9	4
Henry bog.....	10	..	1	9	..
Fauntleroy bog.....	10	..	3	6	1
Echo Lake bog.....	5	2	3
Green Lake bog.....	10	10
Mount Constitution bog.....	3	3	..

It will be noted that the Green Lake bog is the only one whose water allowed the production of root hairs that were normal as to length and abundance. It seems evident that this lack of toxic effect is a result of drainage. Of the 44 plants grown in water from undrained bogs, 8 plants (18 per cent) produced no root hairs, while 29 plants (66 per cent) produced root hairs that were much stunted, and 7 plants (16 per cent) produced root hairs that were slightly stunted.

The above table is based on the roots produced within the first 14 days; these roots were invariably shorter than those produced in tap water within the same time. The new roots that started after that time approximated the length of the roots of plants grown in tap water and produced root hairs that were longer and much more abundant, in many cases approximating normal. The tops of the bottles in which these experiments were carried on were not closed, the surface of the water being exposed freely to the air. DACHNOWSKI (2) found that aeration reduced the toxic effect of bog water from Cranberry Island (Ohio).

In addition to the tests made on bog water and tap water the following tests have been made on other waters of the region: Echo

Lake (5 plants), bog spring on Mount Constitution (3 plants), Mud Lake (10 plants), well water at Friday Harbor, Washington (25 plants). In every one of these cases the root hairs were normal. The water from Echo Lake was dipped up by the writer while standing on the edge of the Echo Lake bog; it was obtained at a distance of 15 feet from where the water from the Echo Lake bog was obtained. The bog spring on Mount Constitution referred to emerges from the side of the mountain and its water seeps into the swamp which gradually merges into the bog. It has the coffee color characteristic of bog water, but not to so marked a degree as the water obtained from underneath typical bog vegetation.

Mud Lake is so close to Lake Washington that the two are connected during the winter season. It is a circular lake about 880 m. in diameter. There is some bog vegetation near its southern end, and the situation of this vegetation appears to be in a general way similar to that of Buckeye Lake bog in Ohio described by DACHNOWSKI (5). The water used was obtained from the edge of the lake at a distance of 90 m. or more from the bog vegetation. The well water used at Friday Harbor was obtained from a surface well near the Puget Sound Marine Station. This is called "tap water" in table I, since the effect of the two has been found to be identical.

Plants were also grown in several solutions which it was expected would prove toxic. The following list of substances was found to produce stunting of the root hairs of *Tradescantia* of an amount and kind comparable with the effect of undiluted bog water: sea water diluted with three times its volume of tap water; carbolic acid, 0.001 per cent; formalin, 0.001 per cent; gelatin, 0.001–0.002 per cent; tea; coffee. In undiluted sea water no roots developed. Stronger solutions of carbolic acid and of formalin entirely inhibited the development of roots.

It is of course possible that formalin might develop from the slow decay of woody materials in the bog in the absence of oxygen, but I have not found any evidence of its presence in bog water. We might reasonably expect, also, that tannin would be found in bogs, but we have no direct evidence that it is a factor in limiting bog floras.

The effect of dilution with tap water was tried with the results shown in the following table:

TABLE II

THE EFFECT UPON ROOT HAIRS OF TRADESCANTIA OF BOG WATER DILUTED WITH TAP WATER

Bog	No. OF EXP.	AMOUNT OF DILUTION	ROOT HAIRS			
			Normal	Slightly stunted	Much stunted	None
Seattle bog.....	1	$\frac{3}{4}$	1
Seattle bog.....	11	$\frac{1}{2}$	11
Henry bog.....	10	$\frac{1}{2}$	7	3
Fauntleroy bog	10	$\frac{1}{2}$	10
Fauntleroy bog	5	$\frac{1}{4}$	5
Fauntleroy bog	10	$\frac{1}{10}$..	5	4	1

From this it appears that the toxin is present in such small amounts that slight dilution greatly decreases the toxic effect. This is in line with the results obtained by LIVINGSTON (7) on *Stigeoclonium*.

Three samples of water from the Henry bog were boiled until each was reduced to one-eighth of its original volume. *Tradescantia* cuttings were placed in them. Few roots started, no root hairs were formed on them, and the plants soon died.

The effect of filtering bog water from the Henry bog through filter paper was tried. The water was collected on October 10, 1911, and three plants were grown in it. They all produced normal root hairs.

A preliminary investigation was made as to the presence and activities of bacteria in the Seattle bog and the Henry bog. Briefly the results may be stated as follows.

1. Beans, peas, and corn decay just as readily in bog water as in tap water.

2. Fresh beef decays a little more slowly in bog water collected in a sterilized jar and kept sealed than it does in tap water under the same conditions.

3. The amount of difference in the rate of decay of pieces of fresh beef buried in bogs and of other pieces buried in swamps is very slight, it being a little more rapid in swamps.

4. Bacteria were found in every case in both bog water and peat collected under sterile conditions. Some of the specimens of peat were collected from as great a depth as 75 cm.

5. *Bacillus subtilis* and *Pseudomonas liquefaciens* were identified in cultures made from surface waters in the Seattle bog.

TRANSEAU (9) found bog waters to be teeming with bacteria. DACHNOWSKI (4, 5) has found bacteria abundant and has given his attention largely to their physiology. Apparently the position that bog waters are very strongly antiseptic is no longer tenable.

Discussion

Suggestions offered by three other investigators (LIVINGSTON, DACHNOWSKI, and COVILLE) bear on the theory stated at the beginning of this paper. In 1905 LIVINGSTON (7) concluded that there were chemical substances present at least in some bog waters that affected the alga that he used (*Stigeoclonium*) as did poisoned solutions, and that these substances are not related directly to the acidity of the water. He concludes that "the stimulating substances here demonstrated may play an important rôle in the inhibition from bogs of plants other than those of xerophilous habit." In 1909 DACHNOWSKI (3) stated his belief "that there are present in bog water and in bog soils injurious substances which are, at least in part, the cause of xerophily in plants and of decreased fertility in bog soils." In 1910 COVILLE (1) stated that "the swamp blueberry (*Vaccinium corymbosum*) grows in peaty soils which contain acid or other substances poisonous to plants. As a protection against the absorption of amounts of these poisons great enough to prove fatal, this plant, like many other bog and acid-soil plants, is devoid of root hairs and consequently has a restricted capacity for absorbing soil moisture." In 1911 DACHNOWSKI (5) words his theory a little differently and speaks of "the toxicity of the habitat and its consequent physiological aridity and selective operation on forms striving for occupancy." In the same paper DACHNOWSKI says that "the reduced absorptive capacity of the plants is not a consequence of the absence of root hairs or of a smaller absorbing surface."

It is thus seen that LIVINGSTON suggested that bog toxins

excluded certain plants from bogs, but did not express any opinion on root hairs, while COVILLE stated the theory that certain plants were devoid of root hairs as a protection against bog poisons, but does not give an opinion whether the bog habitat as it at present exists caused the loss of these root hairs. Neither does he express any opinion as to how mesophytic plants are kept out of bogs. It is to be borne in mind that COVILLE was working on a specific economic problem and evidently did not concern himself, in the paper quoted, with questions of pure science. DACHNOWSKI at first thought that toxins caused xerophily in bog plants and later that the toxicity caused bogs to exercise a selective operation, but does not suggest any injurious effect of bog toxins on root hairs as the cause of such selective operation.

TRANSEAU'S work (10) would seem to suggest that *Larix laricina* is adapted to the Michigan bogs because it can still live after the loss of its root hairs and even after the destruction of the cortical tissues of its roots. *Larix*, however, is not a genus that is universally characteristic of bogs as are such genera as *Ledum*, *Kalmia*, *Oxycoccus*, and *Vaccinium*. There seems to be room for doubt as to the cause of the death of the root hairs and of the cortical tissues of the roots of *Larix* in the Michigan bogs. It is possible that they may be killed by a toxin and attacked by a saprophytic fungus afterward. It is also possible that they may have been killed by a parasitic fungus.

Definite conclusions as to the relation of the toxicity of the bog habitat as a cause and the stunting of root hairs as a result cannot, of course, be drawn from the results obtained from the use of water from six bogs on a single species. Further work must be done with other bog waters and other plants to show how far these two things are related as cause and effect. The question of how bog plants came to be devoid of root hairs is quite a different question from that as to why mesophytic plants are now excluded from undrained bogs. DACHNOWSKI, who in 1909 (3) believed in the activity of bog toxins in causing xerophily in bog plants, states (5) in 1911 that "during the glacial period most species common to bogs skirted the ice sheet." Whether these plants were under bog conditions at this time or whether their distribution was related

to low temperatures only does not seem to be settled. Evidently extremely low temperatures must be reckoned with as one of the factors that determine the characteristics of these plants in past ages, and the same is true of bog plants growing in the extreme north in post-glacial times. We certainly are not justified in concluding that bog conditions as they exist today in temperate regions are the cause of xerophily in bog plants. There does seem to be ground for the belief that certain plants having hairless roots and other xerophilous structures are able to live in bogs, while other plants that normally have root hairs and possess in general a mesophytic or tropophytic structure are kept out of the bogs by these toxins.

It now seems well established that the inhibition from undrained bogs of plants other than xerophytes is not caused by acidity as such (H ions) (LIVINGSTON 7), nor by low osmotic pressure (LIVINGSTON 6), and that it cannot be correlated with low temperatures or strong drying winds (DACHNOWSKI 5), or directly with lack of aeration. Although the toxic effect of bog waters does disappear with continued aeration (DACHNOWSKI 2), it seems evident that the presence of air destroys the toxic substances that are present in bog water, and that the mere absence of air from water does not render it toxic. The fact that DACHNOWSKI (5) found that the toxic effect of bog water can be removed by filtering it through agricultural soils and that the toxic effect was then present in the soil used as a filter seems to settle the point. Whether the toxic effect of bog waters is due to one substance or to several we do not know. Nor do we know positively that it is always due to the same substance or mixture of substances. Undoubtedly the toxic substances are organic, and the problems of organic analysis involved are beyond us at present.

What the source of the toxin (or toxins) is we do not know definitely. There seem to be at least three possible sources: (a) excretion products coming into the substratum from plants growing in the bog, (b) products resulting from decay in the absence of oxygen, (c) excretion products of bacteria. Since it is probable that many other fungi are associated with the bacteria in bogs, it seems scarcely possible to distinguish sharply between (a) and (c).

Since *Sphagnum* is the one macroscopic plant always present in bogs, our attention would naturally be directed to that. Since the presence of *Sphagnum* and the lack of drainage are the two conditions necessary for the formation of bogs, it seems probable that in this combination is the place to seek for the production of the toxin. Bacteria, however, seem to be always present in bogs and their excretion products are to be taken into account.

DACHNOWSKI (5) finds reason for believing that bacteria are active agents in enabling peat bogs to admit certain plants and exclude others. As the same investigator (4) has suggested, the large number of chemical and biological agents present may react collectively with the results of decomposition. Since it has been found by DACHNOWSKI (3) that the presence of a considerable amount of a finely divided insoluble substance destroys the toxic effect of bog water, it seems possible that the absence from bogs of ordinary insoluble soil substances may be a factor in the production of toxicity in bogs.

DACHNOWSKI (5) has given recently a historical summary of the theories of the causes of the xerophilous character of bog plants. In this summary he says "LIVINGSTON suggests the presence of chemical substances not in direct relation to the acidity of the soil as acting on the vegetation. Another explanation, that of the toxicity of the habitat and its consequent physiological aridity and selective operation upon forms striving for occupancy, has been offered by the writer of this paper." In the paper above quoted LIVINGSTON says "the result of these tests is, briefly, that many bog waters act upon the plant [*Stigeoclonium*] like *poisoned* solutions." Again, he says "diluting the . . . samples . . . with distilled water or with a weak nutrient solution decreases the *toxic* effect." In his summary he says "the *stimulating* substances here demonstrated may play an important rôle in the inhibition from bogs of plants other than those of xerophilous habit."

It seems to the writer that the toxin theory of the cause of the exclusion from bogs of plants other than certain xerophytes originated with LIVINGSTON. The theory has been greatly extended and a wealth of experimental data given to support it by DACHNOWSKI,

and the present paper contributes the suggestion that the toxins act through their stunting effect on root hairs.

The bog problem was suggested to the writer by Professor THEODORE C. FRYE, of the University of Washington, and he has had the advantage of his criticism and advice as well as that of Dr. JOHN WEINZIRL, bacteriologist in the same department.

Summary

1. *Tradescantia* grown in bog water shows stunted root hairs.
2. *Tradescantia* grown in water from open lakes and springs immediately adjacent to bogs shows normal root hairs.
3. *Tradescantia* grown in water from drained or partly drained bogs shows almost normal root hairs.
4. The stunting of root hairs of *Tradescantia* by bog water is comparable with the stunting of them by exceedingly dilute solution of sea water, of formalin, of tannic acid, of gelatin, of coffee, and of tea.
5. The stunting effect of bog water on root hairs of *Tradescantia* disappears when it is diluted with an equal volume of tap water and in some cases when diluted with one-half its volume of tap water.
6. The stunting effect of bog water on root hairs of *Tradescantia* may be increased by boiling the water down to a fraction of its original volume.
7. Many typical bog plants have no root hairs.
8. There seems to be a toxin or toxins in bog water whose effect disappears with drainage of the bog.
9. Possibly this toxin inhibits mesophytes from bogs by reducing the amount of absorptive surface exposed by the root system.

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